

EVOLUTION OF CARBON DIOXIDE AT THE FLOOR OF A HYLOCOMIUM MYRTILLUS TYPE SPRUCE FOREST

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Havas, P & Mäenpää, E. 1972: Evolution of carbon dioxide at the floor of a *Hylocomium Myrtillus* type spruce forest. — *Aquilo Ser. Bot.* 11: 4—22. The evolution of carbon dioxide at the floor of a spruce forest situated in the boreal coniferous forest zone was measured using a URAS device. The CO₂ content at the dwarf shrub level under the snow, particularly in the late winter, may be up to three times higher than the corresponding value in the free atmosphere. The evolution of CO₂ under the snow in the winter is of an order capable of measurement, and it continues even after the temperature has dropped below 0°C. Dark respiration experiments carried out on bilberry shoots show that respiration intensity is clearly less in the winter than at the same temperature in the summer, particularly the early summer.

The theoretical CO₂ production at the HMT forest floor was calculated for different times of the year. It appears that in a forest of this type the proportion of plant respiration is high in comparison with net primary production, this being due mainly to the long winter, during which the temperature of the humus is not very low. In summer biological activity is impeded by the coldness of the humus and the lack of nutrients, which result in the growth of an underground biomass.

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1. Introduction

Forests of the *Hylocomium myrtillus* type are among the most peculiar in the coniferous forests of the northern boreal zone (the northern half of the northern taiga; cf. Ahti & Hämet-Ahti & Jalas, 1968). Their problematic character has made them an object of constant scientific interest; the succession of HMT forests and the low productive capacity of their trees have been particularly puzzling to investigators (see e.g. Heikinheimo 1920 and 1922, Teivainen 1952, Sirén 1955).

Since it is necessary to obtain more data on production as a whole, energy flow, the nutrient cycle, and the circulation of water before an overall picture of the HMT ecosystem can be outlined, investigations were started in an HMT forest in Northern Finland in 1967, and are being carried out as part of the International Biological Program (see Havas, 1971a and 1971c).

The main characteristics of HMT forests include the thick, raw, humus layer (=mor) with low nutrient content and the dense, well developed moss cover. The biomass of the field layer mainly consists of dwarf shrubs, notably the bilberry (*Vaccinium myrtillus*). Any attempt to explain the formation of humus in such a forest or the ecology of the whole forest floor must take into account such factors as productivity formation of litter, and decomposition rate. An additional measure proposed recently and applicable at least in theory is the production of carbon dioxide. Sirén (1955), in his comprehensive work on the HMT forests of Lapland has shown that measurements of CO₂ production provide a great deal of valuable information on the ecology of these forests.

The purpose of the present work is to fill in some of the gaps in our existing knowledge

of the CO₂ economy of HMT forests. Special attention has been paid to winter conditions, because there is very little information available on questions such as the CO₂ balance under the snow during long winters. The work involved measurements both of the dark respiration rate of some plants at different temperatures and at different times of the year and of the CO₂ evolution of entire sections of the forest floor (including the plants). Using the results of these measurements, and information obtained on the temperature of the forest floor at different times of the year, it is possible to sketch an overall picture of the liberation of CO₂ during the course of the year.

Since the methods employed are in many ways inadequate, possibly even liable to error, and since the amount of background information available at present is not nearly sufficient, the description that can be given of the evolution of CO₂ in the HMT forest remains incomplete and predominantly theoretical.

2. Description of research site

The forest investigation is situated just south of the arctic circle (66°22'N) close to the eastern border of Finland in the Oulanka National Park in the municipality of Kuusamo. This region falls within the northern boreal zone of the coniferous forest region (Kalela 1961, Ahti & Hämet-Ahti & Jalas 1968). The mean annual temperature at Kuusamo is about 0°C, and the annual amplitude of mean monthly temperature 28—29°C (Kolkki 1966). Annual precipitation amounts to a little over 500 mm. The permanent snow cover falls around Nov. 1st and disappears around May 15th (Suomen Kartasto 1960).

The forest itself is situated on a SW slope (exposition appr. 9°) about 270 metres

above the sea-level. The trees, in particular, already begin to resemble those of the forest limit region, for at this point the forest limit rise only about 200 m above the level of the site. The trees are almost exclusively spruces (*Picea abies*). The average age of the dominant trees is 250 years and the average height 16 metres. The cubic volume of tree stems is appr. 125 m³/hectare. The trees are situated some distance apart and have short branches, so that about 70 % of the forest floor remains beyond the protection of the branches. The forest is in a natural state and reached a climatic climax situation long ago. The forest can be regarded now as representing the »post-climax stage» (cf. Sirén 1955).

The results presented here apply only to the open areas between the trees. The ground vegetation of the site is quite mosaic in appearance, the main reasons for this being the ecological differentiations brought about by the trees and the microtopography (hummocks, etc.). These are great differences between the areas beneath the trees and the open areas, particularly as regards rainfall, thickness of snow cover and consequently, winter soil temperature (cf. e.g. Tamm 1950, Teivainen 1952, Sirén 1955, Yli-Vakkuri

1960 and Havas 1965). The number of species in a *Hylocomium Myrtillus* type spruce forest is in general low. The field layer of the open areas is clearly dominated by *Vaccinium myrtillus*, whose biomass above the moss layer, before the leaves are shed in the late summer, is about 130 g/m². *Vaccinium vitis-idaea* (corresponding biomass 45 g/m²) and *Empetrum hermaphroditum* (corresponding biomass 25 g/m²) are also well represented in the field layer even in the open areas. The proportion of other dwarf shrubs and of herbs in the total biomass is small. Their biomass above the moss layer amounts to only 15 g/m². The moss growth in the open areas, on the other hand, is uniform and thick (living parts 6–8 cm high), the most important species being *Pleurozium schreberi* (biomass 144 g/m²) and *Hylocomium splendens* (biomass 131 g/m²). The total biomass of the other mosses (and lichens) is about 79 g/m².

In the forest investigated the humus of the open areas is nearly 13 cm thick in the summer; in the winter it is somewhat compressed by the snow. The humus layer consists of raw humus. Rhizomes, roots, undecomposed basal parts of plants, and fungal hyphae intertwine in it to form a relatively compact,

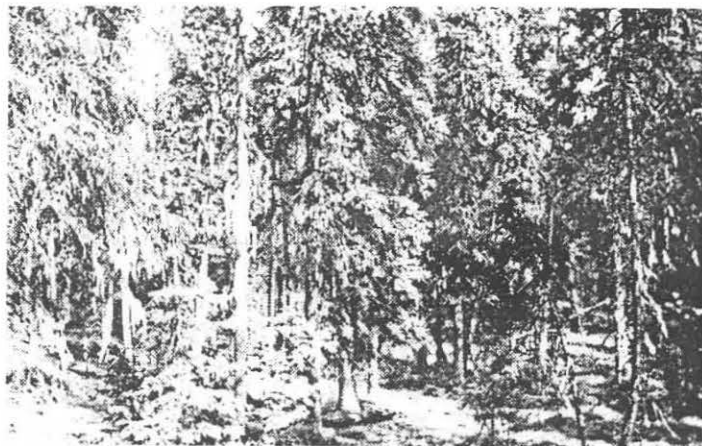
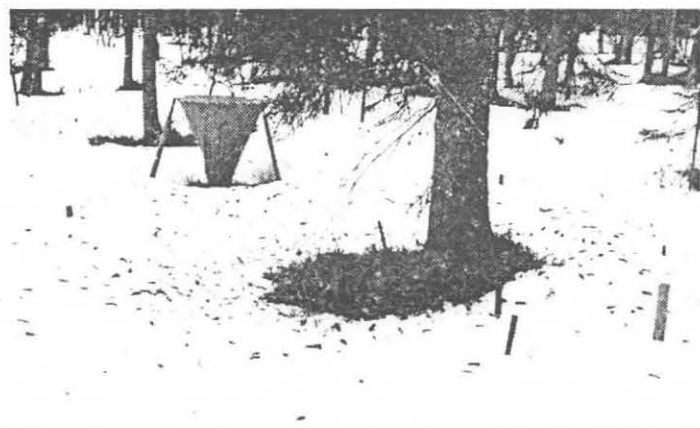


Fig. 1. The *Hylocomium Myrtillus* type forest investigated in Kuusamo (left: in the late winter, May 13th, right: in the summer).

turf-like mat. Most of the species of the field layer are mycorrhizal plants. The biomass of plants present in the humus of the open areas has not yet been fully analyzed, but it seems to be much more abundant than the above-ground biomass. The humus of the open areas contains a total of 1000 g of roots and rhizomes in 1 m². Most of the living biomass in the humus consists of the rhizomes of dwarf shrubs, mainly the bilberry. The proportion of spruce roots in the open areas is small compared with the areas in the immediate vicinity of the trees.

The humus is naturally acid (average pH 4.7) and relatively poor in nutrients, as can be seen from table 1.

Table 1. Nitrate nitrogen and phosphor (mg/l) content, amounts of certain exchangeable cations (meq/l) and pH values in the humus layer and horizon C of the forest studied.

	NO ₃ -N	P	K	Ca	Mg	pH
Humus (A ₀₀ + A ₀)	67	24	2.53	16.62	6.17	4.65
Horizon C	44	5	0.77	43.01	18.50	6.25

Since the bedrock in this region is relatively rich in nutrients, horizon C contains more calcium and magnesium than the humus. When ground water approaches the surface, as it does chiefly in the spring, but also during summer rains, it provides the plants with nutrients from horizon C. As a counter-effect, the water from the melting snow in the spring washes nutrients deeper down from the surface. Since most of the roots never reach beyond the surface layers of the humus, the underlying thick humus layer succeeds in isolating most plants from the more nutrient mineral soil. The pH value of the humus, for example, is only slightly higher than the values reported by Aaltonen (1925) and Teivainen (1952) from the HMT forests of northern Finland, and even lower than the pH values reported by Sirén (1955).

The humus of HMT forests is nearly always relatively moist, because the forest climate is fairly humid, the humus is cold (cf. table 2), and ground water occasionally rises to near the surface. The water content of the humus is about 70 % of dry weight in the summer and 75 % in the winter; the winter figure is, however, based on only a small number of measurements.

3. Methods

The CO₂ measurements were carried out in the laboratory, using a URAS II infrared gas analyzer. During the winter of 1969—1970 and until March during the following winter the air and soil samples (including the plants) were brought to Oulu, being kept at their original temperature during the transportation. At other times the measurements were made at the Oulanka Biological Station in the immediate vicinity of the site.

A. Analyses of CO₂ under the snow

Three frames measuring 50x50x20 cm and covered with coarse sackcloth were placed on even ground (no hummocks or depressions) on open areas between the trees before the first snow-fall in the autumns of 1969, 1970 and 1971. The sackcloth does not prevent exchange of gases, though it does prevent snow from accumulating inside the frame. Thus there was an above-ground air space at the dwarf shrub level, from which air samples could be obtained in the winter. Care was taken to avoid trampling the snow around the frames. It could be seen that the snow above the sack cloth did not freeze any more than the lower parts of the snow cover to in general, which seems to imply that the exchange of gases between the air space and the snow was probably normal (cf. Scholander et al. 1953). Each air sample was drawn off through a 10 mm thick plastic tube fitted to the frame, using a manual rubber pump, and was contained in a pair of polyethylene (0.03 mm) bags one inside the other, the "beachball" technique, cf. Janač et al. 1971, p. 170). Since it was not known whether the CO₂ content of the air in the

bags might tend to vary to balance that of the free atmosphere, the apparatus was tested by filling the bags with gases of known CO₂ content (114 and 494 ppm of CO₂). Some of these were kept in warm conditions, some in cold conditions. When two bags were used together, the CO₂ content of the air did not change noticeably during the first 48 hours, at which point the CO₂ content in the bags had changed by about 15–20 ppm. Whenever samples were obtained from the frames, a control sample was taken from the free atmosphere, but as the CO₂ content of the control samples remained essentially the same throughout the winter, these values are not presented in the tables.

The CO₂ content of the samples was measured using URAS device at the latest 5–10 hours after collection, forcing the air into the analyzer with a diaphragm pump at a flow rate of 30–40 l/h. As the actual range of the URAS device is 100–500 ppm, a special system had to be set up for contents exceeding 500 ppm: The sensitivity range of the device was adjusted, and the results were calculated using the experimental coefficients thus obtained. The coefficients were determined separately for each analysis and were checked by mixing gases with known CO₂ contents and gases for which the content had been calculated. Since the scale of the URAS model available was non-linear, the measurement error was ± 15 ppm within the range 500–1000 ppm and about 30 ppm within the range of 1000–2000 ppm. These figures include the variation of the test gas (494 ppm), reported by the manufacturer to be ± 9 ppm.

B. Experiments to determine CO₂ evolution rate under snow

In January 1971 five bottomless plexiglass chambers (30x30x10 cm) were placed under the snow among the ground vegetation of the open areas, with 2 plastic tubes from of each chamber to the surface of the snow. In this case some snow remained on the mosses within the chambers. Between May 14th and 18th 1971, when the snow cover was about 40 cm thick and moist (temperature of snow and soil surface about 0°C), the following measurements were carried out.

Air samples from each chamber were first drawn into polythene bags (initial values). Then a continuous stream of air was allowed to flow from a pressure

vessel (282 ppm CO₂) into the chamber at a rate of 60 l/h through one of the tubes. Air simultaneously passed out through the other tube. Thus there was some excess pressure in the chamber (cf. e.g. Haber 1958, p. 115–116). Samples of the out going air were drawn into polyethylene bags by means of a suction pump (rate 60 l/h) 30, 60, 90 and 120 minutes after drawing off the initial value samples. It took about 5 minutes to fill each bag, after which the procedure was repeated for the second chamber and similarly for all the remaining ones. The CO₂ content of the air in the bags was analyzed immediately at the Oulanka Biological Station, using the method described above for the samples obtained from under the snow.

When consecutive samples obtained from one place have show practically the same CO₂ values the CO₂ content of the air can be considered to have settled at a certain level. The difference between this level and the CO₂ content of the air pumped into the chambers reflects the liberation of CO₂ taking place under the snow. Under a snow cover of about 40 cm photosynthesis is probably nonexistent due to the lack of light.

C. Experiments on the dark respiration of the bilberry and HMT-mosses in laboratory conditions

Measurements of dark respiration were carried out in connection with the photosynthesis experiments, using a URAS II device. The main attention was focussed on the respiration of the bilberry (*Vaccinium myrtillus*). The experiments were started as soon as possible after obtaining the samples, and carried out on excised shoots 10–15 cm long. The respiration values thus apply only to the aerial parts; the respiration of the rhizomes and roots present in the humus was not measured. During the experiment the excised shoots were kept in thermostatically controlled chambers with their lower ends in water. The measurements were made by alternately switching the light on and off in the chambers, so that the values actually recorded may be slightly different from those which would be obtained in the chambers ^{which} were kept dark throughout the experiment. The temperature of the chambers was increased in steps and respiration rate was measured for each new temperature value. The rate of flow of the air was about 60 l/h.

The dark respiration of mosses was measured according to the same principle, using only material collected in the winter. The mosses were not classified according to species, small mixed samples being used just as they were obtained from the open areas. Tufts of moss were not disentangled. In order to keep the degree of compactness of the mat as nearly natural as possible, no attempt was made to disentangle the tufts of moss. The mosses were kept fresh in the experimental chambers, but they were not kept in water as were the bilberry shoots. The mosses did not dry noticeably during the experiment, for the temperature of the chambers never exceeded $+10^{\circ}\text{C}$. Rate of flow of the air in the moss experiments was about 40 l/h.

D. Experiments on the evolution of CO_2 from soil samples in laboratory conditions

The first experiments were carried out using the URAS II device and associated chambers with a diameter of 30 cm, in which the soil samples measuring 25x25 cm (including dwarf shrubs and mosses) were placed. The samples were taken along the junction of the humus and mineral soil, themselves containing no mineral soil. The respiration of such large samples, however, is so great, particularly at temperatures above 5°C , that the flow of air could not always be maintained at a sufficient level to keep the readings within the scale of the URAS device. Thus these large chambers were soon rejected in favour of smaller ones with a diameter of 15 cm, so that the soil samples measured 13x13 cm at the most, but were still thick, enough to include the whole humus layer. The results did not differ essentially from those obtained by using the larger chambers.

The chambers were kept in a glycol-water bath whose temperature was controlled by means of a thermostat. Usually, each experiment was started at approximately the temperature of the sample in natural conditions. In summer, however, the temperature was brought down below the initial value towards the end of the experiment. The CO_2 readings were obtained following a temperature change of $3-5^{\circ}\text{C}$, after the temperature had again settled to a more or less constant value. The temperature was read from the humus at a single point in the centre of the soil sample by means of a thermoelement.

Owing to the arrangement of the experiment, the results may easily contain errors. At least the following possibilities should be mentioned:

- 1) The presence of excised parts of plants (roots, rhizomes etc.) in the sides (and the bottoms) of soil samples causes the readings to differ from those obtained in natural conditions.
- 2) The water content of the humus and the plant of the soil samples varies. In the winter the average water content of the humus is 75 % of dry weight, while on the summer it is 70 %, but slight variations occur particularly in the summer.
- 3) The degree of compactness of the humus varies according to the circumstances. In the winter the humus is usually compressed by the snow and is therefore more compact than in the summer. Thus aeration differs from sample to sample.
- 4) In the experiment chambers air has access to the sites of the samples, which is naturally not the case in normal conditions. Comparative experiments, in which the sides (and the bottoms) of the samples were covered with plastic film, showed, however, that the results are not greatly affected by this abnormally effective aeration. Furthermore, soil respiration is probably most intensive in the topmost layer of humus (cf. e.g. Sirén 1955 and Kunze 1969), which is better aerated than the lower parts even in natural conditions.
- 5) The flow rate of air used in the experiments was about 60 l/h (slight excess of pressure in the chambers), which naturally does not correspond to real conditions, particularly in the winter when the flow of air is almost non-existent under the snow and the CO_2 content may become quite high. This, in turn, may affect the respiration of the sample (antirespiration, cf. Steeman—Nielsen E., 1953).
- 6) When the temperature of a soil sample was altered, it was difficult to achieve a uniform temperature in the whole sample. In some cases not a long enough was allowed for the temperature to stabilize in the different parts of the sample.
- 7) Since the measurements were started at low temperatures, the first CO_2 readings at these temperatures may be too high, for some CO_2 may be liberated from the soil as the flow of air in the chambers begins.

Such sources of error, some of which are syste-

matic, others random, call for a careful and critical interpretation of the results.

4. CO₂ content under the snow

Figure 2 shows the variation of CO₂ content under the snow in the open areas of the HMT forest during three winters. The measurements showed that the CO₂ content of the air under the snow varies considerably in the course of the winter. Measurements for three winters are therefore hardly sufficient to yield reliable results. Moreover, there were only three points at which measurements were made, and, as the figure shows, the CO₂ content may differ considerably between the three points at any one time.

The variation is naturally due to a number of factors, the most important of which are the temperature under the snow, the structure and water content of the snow (cf. Scholander et al. 1953), the thickness of the humus, and the amount and type of vegetation cover. Winds may similarly affect aeration even under the snow, but this factor is less influential in the forest than in treeless

areas. The CO₂ values recorded by Kelley & Weaver & Smith (1968) on the tundra are, partly for this reason, partly for the other reasons enumerated above, lower than the values obtained from the present HMT forest.

Although the temperature of the humus under the snow does not vary much during the winter, even a small change may affect the accumulation of CO₂ in the course of time. It must be pointed out, however, that the temperature of the humus or the dwarf shrub level is not of crucial significance for the accumulation of CO₂, which seems rather to depend on certain other factors. The results reveal the interesting phenomenon that in the surface part of the soil, including the plants, respiration takes place even when the temperature of the humus and the dwarf shrub level remains permanently below 0°C. During the early winter the CO₂ content under the snow in HMT forests tends to be low, usually under 600 ppm. Variation between the different points of measurements is similarly quite small at this time of year. From February

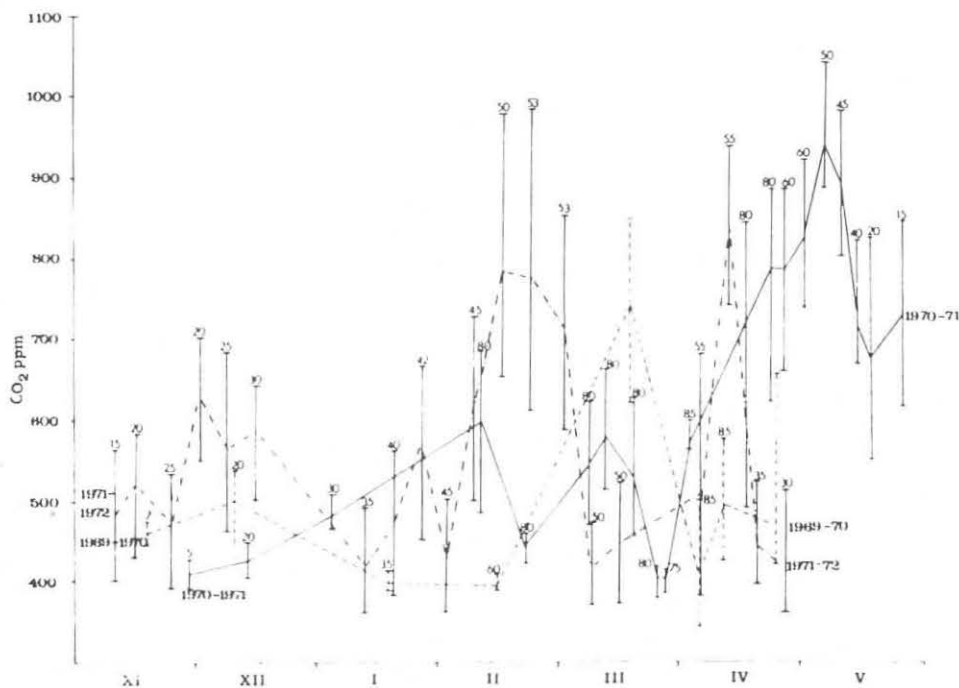


Fig. 2. CO₂ content under the snow in the HMT forest during the winters 1969—70, 1970—71 and 1971—72. The ends of the vertical lines indicate the extreme values from three measurements. The average thickness of snow cover at the points of measurement is indicated above the vertical lines.

onwards the CO_2 content begins to rise as the snow cover becomes thicker and more compact. Unfortunately, insufficient measurements were made of the hardness and density of snow in this forest to show any correlation with CO_2 content. Usually, however, the snow becomes compact towards the spring, and a hard crust may be formed on its surface even in forests.

At the end of March and the beginning of April 1971 an obvious steady rise began in the CO_2 content under the snow. The peak values, occasionally exceeding 1000 ppm, were reached at the beginning of May. It seems therefore, that snow in the late winter is a fairly effective insulator as regards both temperature and gas exchange (cf. Scholander et al., 1953). This phenomenon was also apparent in the winter of 1971–72: the highest CO_2 -concentrations were recorded when the snow cover was thickest (the latter half of February and the middle of April). The snow cover was generally thin during that winter.

At the time of the melting of the snow the CO_2 content of air begins to decrease. This may be due to the fact that not only does the snow cover become thinner but the water present in the snow binds some of the carbon dioxide. Yet CO_2 values as high as 700 ppm were still recorded under 15–20 cm of snow in May 1971. This seems to suggest that the evolution of CO_2 is more abundant in the spring than under the thin snow cover late in the autumn. The buds of the bilberry, for example, clearly begin to swell while still covered with snow (cf. Havas, 1971b).

There are many ways in which high CO_2 values may be significant, for the ecosystem and its subsystems. The high CO_2 content and the corresponding low O_2 content may be harmful to certain animals. The same may apply to plant respiration (antirespiration).

In the late spring, on the other hand, when the snow cover is sufficiently thin a high CO_2 content may help to promote the photosynthesis of plants. About 5 % of full daylight is able to penetrate through a layer of snow 15–20 cm thick. Measurements showed that the light falling on the snow in an HMT forest averaged about 10.000 lux on bright spring days, and in open areas over 20.000 lux. If photosynthesis does take place under the snow in May, it naturally reduces the high CO_2 content.

The above account applies to the areas between the trees. Beneath the trees, where the thin snow cover allows the soil to become cold in the winter and frost to penetrate deep, and where the above-ground biomass is less abundant than in the open areas, the wintertime production of CO_2 is probably much less than it is in the open areas.

5. Rate of CO_2 evolution under snow in natural conditions.

In order to determine the rate of CO_2 production under the snow in natural conditions, the air sampling method described above (chapter 3B) was employed. The experiments were carried out in the spring, when under snow CO_2 evolution appears to be faster than earlier in the winter. There were also technical advantages in attaching the experiment during the melting season when the temperature remains fairly constant.

As can be seen from figure 3, the CO_2 content of the plexiglass chambers placed under the snow in midwinter was very high prior to the experiment. One day was sufficient to treble the CO_2 content of the chambers compared with that of free atmosphere. The air pumped into the chambers reduced the CO_2 content so greatly that a balance was reached within half an hour.

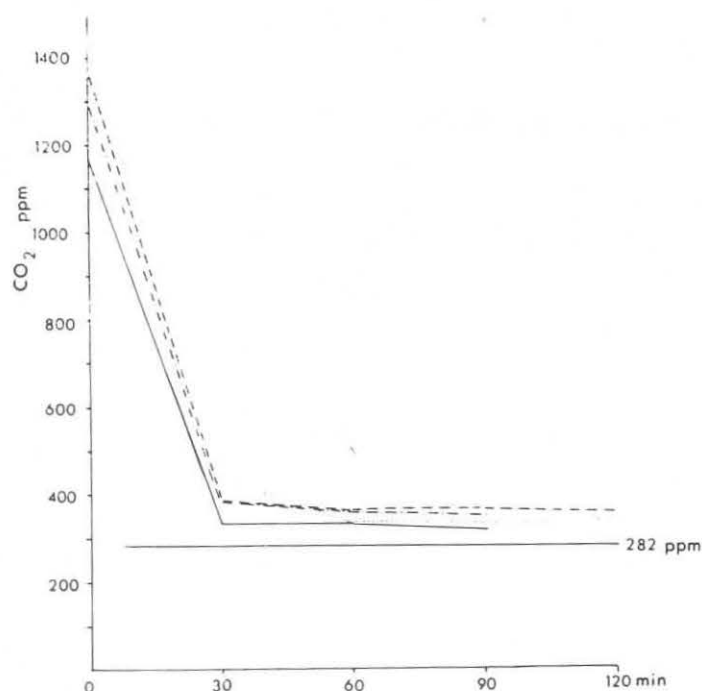


Fig. 3. CO_2 content under the snow at the floor of the HMT forest during the period May 14th — 18th 1971. Continuous line: CO_2 content on May 14th, dashed line May 15th, dashed-dotted line May 17th, and dotted line May 18th. The CO_2 content of each of the five chambers were measured at the beginning of the experiment (0) and after 30, 60, 90, and (on May 15th and 18th) 120 minutes. The lines indicate the mean values of these measurements. The horizontal line 282 ppm show the CO_2 content of the pressurized air entering the chambers. The temperature of the snow was approx. 0°C .

After that the difference between the CO_2 contents of the in-going and the out coming air could be used to calculate the production of CO_2 per time unit and area. No great differences were noted in the rate of CO_2 production between the different days: the lowest mean (May 14th) was $98.0 \text{ mg CO}_2/\text{m}^2/\text{h}$, and the highest (May 17th) 145.0 mg . The mean for all the measurements was $126.4 \text{ mg CO}_2/\text{m}^2/\text{h}$. This value is almost the same as the mean for the readings obtained under laboratory conditions from the soil samples collected in May (measured at a temperature of 0°C), although the dispersion of the latter results was greater (cf. fig. 5).

The present series of measurements shows

that the rate of CO_2 evolution under the snow in an HMT forest around 0°C is of discernible order. It would be necessary, however, to perform more such field measurements in order to obtain reliable information about the rate of CO_2 liberation at different temperatures.

6. Some dark respiration experiments on plants in laboratory conditions.

Figure 4 shows the dark respiration of the aerial shoots of *Vaccinium myrtillus* as revealed in URAS measurements. The mean values are distributed in relatively distinct curves, though the results of individual

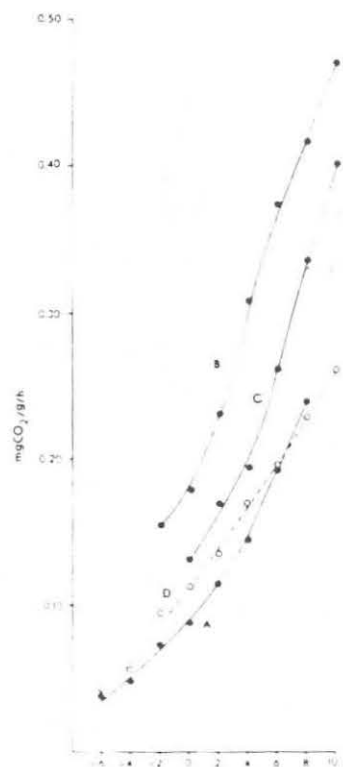


Fig. 4. Dark respiration of the HMT bilberry (*Vaccinium myrtillus*) and mosses at different temperatures under laboratory conditions expressed in mg of CO_2/g (dry weight)/h. A = respiration of the bilberry in winter (November—May), B = respiration of the bilberry in early summer (June—July), C = respiration of the bilberry in late summer and autumn (August—October), and D = respiration of the mosses (chiefly *Pleurozium schreberi* and *Hylocomium splendens*) in the winter (December—March). Each spot represents 10—30 measurements for the bilberry and 6 measurements for the mosses.

measurements (not shown in figure 4) are somewhat dispersed. Figure 4 shows that respiration continues even when the temperature drops below 0°C . The most interesting finding made in these dark respiration measurements was the fairly clear seasonal variation in the respiration intensity of bilberry shoots. Respiration is least intensive in the winter (curve A), but as early as June, occasionally even at the end of May when the snow is melting, respiration is very intensive. The early summer is represented by curve B in figure 4. The most active growth of the bilberry occurs at that time: the leaves appear during June. It appears, therefore, that the new shoots with leaves have higher values for respiration intensity (calculated per unit weight) and for photosynthesis at that time than at the same temperature later in the summer when growth has ceased, to say nothing of the shoots under winter conditions. The late summer is represented by curve C in figure 4. Respiration is less intensive at that time than in the early summer, though still more intensive than in the winter.

Wielgolaski (1970) presents values for the respiration of the bilberry at Hardangervidda in Norway. These values, obtained from shoots in a subalpine birch forest and an alpine area in the late summer, are of the same order of magnitude as these present results for the late summer and the winter.

The Q_{10} of bilberry shoots at the temperature of $0-10^{\circ}\text{C}$ is appr. 3.7 in the winter, 2.6 in the early summer, and 3.1 in the late summer. These values are of the same order of magnitude as those presented by Wager (1941) of arctic plants. Wager (op.c.) observed that the Q_{10} of the rate of respiration of arctic plants is larger in the winter than that of temperate plants, and this seems to be the case in the northern parts of the coniferous forest zone as well.

The respiration of mosses has so far been measured only from samples collected during the winter. The species have not been specified in the material, which consists of collective samples obtained from the HMT open areas, most of their biomass being naturally composed of *Pleurozium schreberi* and *Hylocomium splendens*. The respiration of mosses (fig. 4 curve D) seems to be related to temperature in more or less the same manner as the wintertime respiration of bilberry shoots, though the change in the former is more linear (at the temperatures measured). Comparison of these results with those obtained from the respiration of *Pleurozium schreberi* in the subalpine birch forest at Hardangervidda by Wielgolaski (1970) shows that the present values obtained in the winter are clearly higher than those obtained by Wielgolaski in the late summer. The differences may be due to methodological in accuracies differences in the moisture of the samples, or other such factors. It is also possible that the respiration of HMT mosses may really be quite intensive in the winter, since they continue to grow until late in the autumn.

7. Rate of CO_2 evolution in soil samples in laboratory conditions.

As has already been pointed out (chapter 3D), measurements of this kind involve several possible sources of error and the disparity in the results tends to be great. In spite of this, the results obtained from measurements of CO_2 production in soil samples at different temperatures are presented (fig. 5). Since the measurements carried out were numerous and the results at 0°C largely agreed with those obtained in natural conditions (as reported in chapter 5), figure 5 probably reflects to some degree

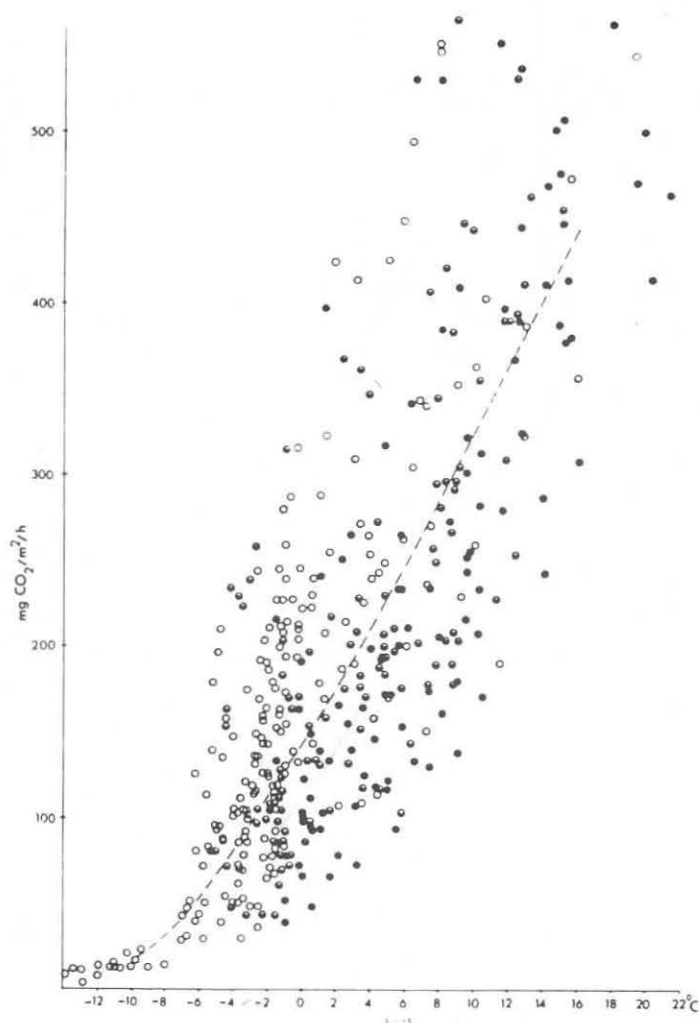


Fig. 5. CO₂ production of soil samples (including plants) at different temperatures under laboratory conditions. Circles = assays made in the winter, partially filled circles = assays made in May, and spots = assays made in the summer. The dashed line shows the approximate median of the values obtained at the different temperatures. This was used for calculating the CO₂ production values of the soil samples presented in Table 2.

the general characteristics of the CO₂ balance at the HMT floor. The measurements were carried out on the initial soil samples, which included the above-ground biomass. The mineral soil, however, which is also known to produce CO₂ (cf. Romell 1928, Sirén 1955), is not included in the samples.

The results of the measurements carried out at three seasons of the year are presented separately, for respiration seems to be slightly more intensive in the winter (fig. 5, circles) than at the same temperature in May or

in the summer (fig. 5, partially filled circles and dots). This finding is contrary to that presented above (ch. 6) for the respiration of aerial bilberry shoots, which is less intensive in the winter than at the same temperature in the summer. Woodwell & Dykeman (1966) maintain that the evolution of CO₂ in the oak-pine forests of the temperate zone is 2–3 times less intensive in the winter than at the same temperature in the spring or in the summer.

Direct comparison of the respiration results of HMT bilberry shoots and soil samples is hindered by the great dispersion of values in the respiration of the soil samples. The measurement units may also lead to differences. Results obtained in the winter may further be obscured by the "stress respiration" frequently noted in cold samples whose temperature is brought up suddenly during the experiment (cf. Bauer & Huter & Larcher, 1969, Larcher, 1969, Kallio & Heinonen 1971). Such factors as water content and compactness, which vary in the samples, probably also increase the dispersion of the results. The HMT humus and moss layers are often drier in the summer than in the winter, whereas the bilberry shoots, for example, contain more water in the summer than in the winter (cf. Havas, 1971b). It has already been mentioned (ch. 6) that the wintertime respiration values of HMT mosses are remarkably high. This finding, if reliable, seems to suggest that the respiration of HMT mosses, or the parts of higher plants present in the humus, or the micro-organisms (e.g. *Fusarium*-species) of the humus (or all of these) is at least slightly more intensive in the winter than at the same temperature in the summer. This difference need not be great, however, for the biomass of the mosses, the humus and the plants present in it is abundant in comparison with the above-

ground biomass. According to Sirén (1955), the conditions for soil respiration in HMT forests, excluding temperature, would be more favourable in the early summer than in the autumn. Kunze (1969), on the other hand, using soil samples in laboratory conditions, shows that CO_2 production in the humus of the spruce forests of Central Europe is most vigorous late in the autumn (October–December).

The problem described above naturally requires further investigation. It can be seen, however, that the CO_2 production of both the above-ground biomass and the whole soil samples is clearly correlated with temperature. Experiments carried out on soil samples give further support to the results which show that CO_2 continues to be liberated at temperatures below 0°C . Other ecological conditions of the surface layers may also affect the production of CO_2 , but in the open areas of HMT forests the moisture content of the humus, for example, varies so little that it is far less significant for the CO_2 economy than is temperature. According to Sirén (1955), however, HMT humus may occasionally be too moist to provide optimal conditions for CO_2 liberation.

8. Production of CO_2 at the floor of HMT open areas during the year

Although the results presented above are doubtful on some points and do not fully represent the natural conditions, it is reasonable to continue by examining the total annual CO_2 production of the open areas. The material presented above proves adequate for such an examination particularly since the temperature and moisture content of the HMT forest floor do not vary very greatly or very irregularly. Especially during the long winters, when no photosynthesis

occurs, the conditions under the snow are fairly stable.

Table 2 shows the monthly values for CO_2 production. Unfortunately the data for biomass are not sufficient to explain the seasonal variation. The mass of the mosses, which accounts for more than half of the above-humus biomass, does not vary appreciably during the course of the year, nor does the mass of the dwarf shrubs, even though, on account of the falling leaves of *Vaccinium myrtillus*, the wintertime-biomass of the dwarf shrubs decreases by about 10–20 % on open places. The biomass of the herbs naturally varies most, but the proportion of these plants in the total HMT biomass, and consequently their part in CO_2 production, is negligible. The final values are calculated from the wintertime biomass values, which are valid for at least eight months of the year.

In the calculations of the respiration of plants and plant groups it has also been necessary to accept inadequate data. The respiration values for all dwarf shrubs and herbs were calculated using the respiration curves for the bilberry presented in figure 4. Thus the values of CO_2 production obtained for dwarf shrubs other than the bilberry may be too great even in the winter months, for *Vaccinium vitis-idaea* and *Empetrum hermaphroditum*, at least, may have a respiration less intensive than the bilberry (cf. e.g. Wielgolaski, 1970). Only values for wintertime respiration were available for the mosses (cf. fig. 4). As has already been noted, these mosses show higher respiration values at low temperatures than the summertime values for *Pleurozium schreberi* reported by Wielgolaski (1970). Thus the respiration values calculated here for the above-ground biomass may be, at least in the summer, somewhat higher than the real values. It

Table 2. Monthly CO₂ production (g/m²) and temperatures (C°) on the forest floor, open places in HMT

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I—XII
Respiration of above-humus biomass ¹⁾ :													
Dwarf shrubs (biomass 250 g/m ²)	9.0	1.8	10.9	14.3	16.2	93.6	95.4	77.4	43.2	25.2	9.0	10.9	406.9
Herbaceous plants (biomass 10 g/m ²)	0.3	0.1	0.4	0.6	0.6	3.7	3.8	3.1	1.7	1.0	0.4	0.4	16.1
Mosses (biomass 300 g/m ²)	13.0	2.2	17.3	19.5	23.8	62.7	67.0	60.5	41.0	25.9	13.0	15.1	351.0
Total for above-humus biomass	22.3	4.1	28.6	34.4	40.6	160.0	166.2	141.0	85.9	52.1	22.4	26.4	784.0
Respiration of soil organic matter, roots and rhizomes	57.4	51.6	62.2	60.4	60.4	66.5	89.9	103.0	85.0	66.8	57.4	62.2	821.8
Respiration of forest floor (open areas) total ²⁾	79.7	55.7	90.8	94.8	101.0	226.5	256.1	244.0	170.9	117.9	79.8	88.6	1605.8
Temperature at dwarf shrub level ³⁾	-4.2	-9.1	-2.6	-1.4	+0.1	+12.7	+13.3	+11.4	+5.5	+0.8	-4.3	-3.1	+1.6
Temperature in middle layer of humus ³⁾	-0.8	-1.3	-0.5	-0.3	-0.2	+5.7	+9.7	+9.7	+6.8	+2.5	-0.6	-0.5	+2.5

¹⁾ The values for the biomass are wintertime values. They include the parts of dwarf shrubs and herbs above and in the living moss layer. The respiration values for all the dwarf shrubs and herbs were calculated according to the respiration curves of the bilberry (cf. Fig. 4) and the temperatures of the dwarf shrubs level. Only one respiration curve was available for the mosses (obtained during the winter months) and the production of CO₂ was calculated using the temperatures of the dwarf shrubs level.

²⁾ Example of the calculations for January: Fig. 5 shows that the CO₂ production of the soil sample at -0.8°C is 94 g/m²/month. The respiration values of the above-humus biomass at -0.8°C (36.6 g/m²/month, calculated from Fig. 4) are substrated from the initial value and the respiration value of the above-humus biomass at temperature on dwarf shrubs level -4.2°C (i.e. 22.3 g/m²/month) is added. Thus 94 - 36.6 + 22.3 = 79.7 g/m²/January.

³⁾ The means are calculated from values measured in years 1969—1971 daily at 2, 8, 14 and 20 a clock.

should further be noted that the respiration values of the mosses were calculated using the temperatures of the dwarf shrub level, which are slightly lower in the winter and slightly higher in the summer than the temperatures of the moss level itself.

During the snowless period (June—October) photosynthesis naturally eliminates part of the CO₂ production. It is therefore impossible to use the results to estimate the amount of CO₂ actually liberated in the summer.

The CO₂ production of the above-humus biomass is naturally very small at certain times during the winter, but during the period of permanent snow cover (December—May) it forms on the average 30 % of the total wintertime CO₂ production of the area (excluding the mineral soil). In the summer the rate of dark respiration of the above-humus biomass rises considerably, for at that time of year the dwarf shrub level is consi-

derably warmer than the humus, and the respiration activity of dwarf shrubs, particularly in the early summer, is high, as was reported in chapter 6. In the winter the situation is reversed. The dark respiration of the above-humus biomass during the whole year is 784 g CO₂/m².

As regards comparison of the respiration rates of the different plant groups presented in table 2, it can be seen that no sufficient grounds for such a comparison exist, for the values are, after all, only calculated and theoretical. In the late autumn and the early spring, for example, the moss level of the HMT forest is often very wet, and the real respiration values may therefore not be in accordance with those presented in the table, which show the contribution of moss respiration to the CO₂ production calculated per unit area to be generally greater than that of the dwarf shrub respiration in the winter (cf. Sirén 1955).

Assuming that 1 g of CO_2 corresponds to 0.614 g of dry matter (cf. e.g. Woodwell & Dykeman 1966) and that the annual respiration of the above-ground biomass in HMT open areas is $784 \text{ g CO}_2/\text{m}^2$, the annual consumption of dry matter would be 481 g/m^2 . It may be estimated that the aerial parts of the undergrowth of HMT open areas (including the mosses and the biomass amongst them) have a net primary production of $100\text{--}150 \text{ g/m}^2/\text{year}$. Gross production would thus be $580\text{--}630 \text{ g of dry matter m}^2/\text{year}$. If this calculation is correct the role of respiration, a significant one, it accounts for $76\text{--}83 \%$ of the annual gross production. This is understandable, however, for the winter is long and it is not very cold under the snow. During the winter (December—May) the above-ground HMT biomass produces about 20% of their total annual CO_2 . Johnson & Kelley (1970) report that in the arctic conditions of Alaska about half of the products of photosynthesis are used for respiration or are eaten by animals, while the other half is either accumulated or respired during the winter.

The present calculations show the total annual CO_2 production in the HMT open areas to be approx. 1600 g/m^2 (excluding the CO_2 production of the mineral soil). These calculations are based on the approximate mean values for CO_2 production in the samples at each temperature (cf. fig. 5), ignoring the small differences observable between the winter and the summer. About $1/3$ of the total production, i.e. $590 \text{ g CO}_2/\text{m}^2$, is liberated during the period of permanent snow cover (December—May), when no photosynthesis occurs. Corresponding data from other sites, particularly in the coniferous zone, are still scarce at the present. Annual values for CO_2 production at the floor of the deciduous forests of the tempera-

te zone are generally $1500\text{--}3000 \text{ g of CO}_2/\text{m}^2$, in other words higher than the present estimates for HMT forests (cf. Wierkamp 1966, Reiners 1968, Woodwell & Botkin 1970). On the other hand, the annual CO_2 production on the arctic tundra may be only $1/10$ of the HMT figure (cf. Johnson & Kelley 1970). According to the review compiled by Wierkamp (1966), CO_2 production at the floor of the oak forests of the temperate zone is $400\text{--}500 \text{ ml/m}^2/\text{h}$, which corresponds to $1\text{--}8 \text{ g CO}_2/\text{m}^2/\text{h}$. If the values were obtained in natural conditions, the effect of the CO_2 production of the mineral soil on them may have been considerable (cf. Romell 1928, Sirén 1955). The CO_2 production figure in the soil samples (including the plants, but excluding the mineral soil) obtained from the HMT forest during the period June—August is only about $0.3 \text{ g/m}^2/\text{h}$. In the winter the difference between the forests of Central Europe and Northern Finland appears to be smaller, which is probably due to the fairly high temperature of the humus and possibly also to the relatively high values for humus respiration noted in HMT forests in the winter (cf. Woodwell & Botkin 1970, and Reiners 1968). In any case, soil respiration continues at temperatures below 0°C , as is shown by table 2, although Sirén (1955) assumes it to cease at 0°C . It is not yet possible, however, to establish the total CO_2 production of the HMT forest, for the CO_2 production of the trees and the mineral soil has not been measured and the conditions prevailing under the trees have not yet been described in sufficient detail. It has already been mentioned that 30% of the total forest area under study consists of ground sheltered by trees. The respiration of the undergrowth and soil of those areas is probably less intensive than it is in the open areas.

As mentioned earlier, the respiration of the

above-ground biomass accounts for a great proportion of the gross production of the forest floor. It has also been suggested that the forest floor (excluding the mineral soil) produces about 1/3 of its total annual CO_2 during the winter. The situation can thus be considered disadvantageous for the net primary production of the HMT forest.

Such »wastage» is due to several factors, primarily to the long winters during which the temperature, particularly in the humus, remains fairly high. The summer conditions are similarly unfavourable, for the humus is relatively cold and biological activity consequently low. Furthermore, the nutrient content of the humus is poor. Thus the part of the biomass of higher plants present in the humus (roots, rhizomes) is considerable in comparison with the photosynthesizing biomass. Against this background it does not seem strange that even the net production of HMT trees, particularly in older forests, should remain relatively small. Under such conditions even the competitive position of the spruce must be weaker than in other types of spruce-dominated forest.

If the dark respiration of the above-ground biomass accounts for 49 % of the total annual CO_2 production of the HMT forest, the contribution of the humus and its biomass must amount to 820 g of CO_2/m^2 . In the summer, when respiration is most intensive, the CO_2 production of the HMT humus and its biomass is 92 mg $\text{CO}_2/\text{m}^2/\text{h}$ in June (humus temperature $+5.7^\circ$), and 134 mg $\text{CO}_2/\text{m}^2/\text{h}$ in July–August (humus temperature $+9.7^\circ$). These values are considerably higher than those reported by Sirén (1955) for the HMT forests of Lapland, which show the CO_2 production of the humus to be 50 mg at $+5^\circ\text{C}$, and 80 mg/ m^2/h areas (including the roots of trees; cf. e.g. real, for the forests investigated by Sirén

(op.c.) are situated further north, and may have poorer nutrient economy than the forest discussed here. Kärenlampi & Mäkinen (1970) maintains that the soil respiration of sub-alpine birch forests in Finnish Lapland is less than 50 mg/ m^2/h at $+5^\circ\text{C}$, and 75–100 mg at $+10^\circ\text{C}$. According to Mäkinen (1971), the soil respiration of the dwarf shrub-pine forests in the timber line region of Finnish Lapland is also roughly of this order. In the spruce forests of Central Europe soil respiration is more intensive than in the HMT forest under investigation here; Haber (1958) and Lieth & Ouellette (1962) report values ranging from 150 to 430 mg/ m^2/h in the summer and autumn.

The biomass in the humus of the open areas investigated is far in excess of the above-ground biomass of the forest floor. The biomass of the humus has not yet been analyzed sufficiently, but roots and rhizomes probably amount to 1000 g/ m^2 in the open areas (including the roots of trees; cf. e.g. Sirén, 1955 and Flower-Ellis, 1971). Almost one half of the living biomass in the humus (in the open areas) consists of bilberry rhizomes though spruce roots account for a considerable proportion in the areas near the trees. The fact that the annual CO_2 production of the humus and its biomass was found to be only 820 g/ m^2 seems to suggest that the respiration of the biomass in the humus is less intensive than that of the aboveground biomass at the same temperature.

The amount of litter and other dead plant material on the open areas of the HMT forests may be estimated at 300 g/ m^2/year . This includes the needle litter of spruces. The decomposition rate of litter, is not yet known, nor is it known whether in HMT forest the litter decomposed completely. But if we assume that no accumulation takes place, the annual CO_2 production of the

litter would be 489 g/m² (calculated according to the method described by Woodwell & Dykeman (1966): 1 g of CO₂ corresponds to 0.614 g of dry matter). This CO₂ figure accounts for more than one half of the annual CO₂ production of the humus and its living biomass. The contribution of the respiration of roots and rhizomes in the humus would accordingly be about 333 g CO₂/m²/year.

In fact, however organic matter probably accumulate slowly over the years in the HMT forest, and thus the CO₂ production of the litter is probably smaller than given value, while the respiration of roots is correspondingly more intensive. The dry weight of the humus (without roots) in our forest is about 8500 g/m² at the present, which means that the total respiration of the humus is slight if compared with the amount of organic matter in the soil.

Since the living biomass of the humus is about 2 times greater than the above-ground biomass on the forest floor in open areas, while the CO₂ production of the former is only 40 % of that of the latter, it follows that the respiration rate of the biomass in the humus must be 4—5 times slower than that of the above-ground biomass. This is, naturally, a very rough estimation based upon inadequate data, and must therefore be considered only preliminary and theoretical.

This reservation applies, to a great extent, to all the calculations presented in this section; they must be considered no more than theoretical. Yet can be concluded that most of the present results seem to fall with the range to be expected on the basis of the literature, though it should naturally be remembered that the literature available on the topic is far from comprehensive, particularly as regards boreal coniferous forests.

9. Summary

Research was carried out in a *Hylocomium Myrtillius* type spruce forest in northern Finland, to investigate the production of CO₂ at the forest floor in the areas between the trees particularly under winter conditions. In the late winter and the spring the CO₂ content under the snow may be very high — occasionally even 3 times higher than normal (cf. fig. 2). Since the temperature variations under the snow are relatively small, the great variation in CO₂ content is probably not so much due to the temperature as to the structure and thickness of the snow cover. Winds may similarly have some effect on the accumulation of CO₂ under the snow even in the forest. A high CO₂ content is likely to have some ecological significance for both animals and plants.

The evolution of CO₂ under winter conditions is of an order capable of measurement. Respiration continues even when the temperature drops below 0°C, and the temperature of the HMT humus under a thick layer of snow generally never falls so low that respiration ceases altogether. CO₂ production at -3°C may be as much as 100 mg/m²/h (cf. fig. 5). In the summer, respiration is naturally much more intensive (about 200 mg CO₂/m²/h at +3°C, and a little over 300 mg at +10°C). The measurements, most of which (with the exception of the series presented in figure 3) were carried out under laboratory conditions, naturally do not represent the real situation. Furthermore, there is a comparatively wide dispersion in the results of the measurements, although the moisture of the HMT humus, for example, does not vary much.

Dark respiration experiments were also carried out on the bilberry (*Vaccinium myrtillius*), the main species of the HMT field

layer. Perhaps the most interesting finding was that the intensity of respiration (per unit weight of shoots) varies during the course of the years (cf. fig. 4): respiration is much less intensive in the winter than at the same temperature in the early summer. Towards the late summer the intensity of respiration declines. A few dark respiration experiments were also performed on HMT mosses, though without specifying species. Such measurements were made only in the winter, when the respiration of the mosses was remarkably intensive compared with results obtained elsewhere in summer.

When the CO_2 production of a given area (including the plants) at different temperatures and at different times of the year is known, it is possible to calculate the annual production of CO_2 . This was done in the present work (cf. table 2), although the data are still inadequate in several respects. The results obtained must be regarded as theoretical, though they are in fact in fairly good agreement with investigations of this kind carried out elsewhere.

Although the respiration values of the different species are not yet known, it can be estimated that the respiration of the biomass above the humus accounts for nearly half of the annual CO_2 production of the forest floor between the trees (excluding the mineral soil). The respiration of the biomass above the humus probably accounts for 80 % of the gross production, the reasons for this being the long winter and the relatively high temperatures under the snow. The total annual production of CO_2 in the HMT floor (excluding the mineral soil) is about 1600 g/m^2 , of which more than a third is produced during the winter. The living biomass present in the humus of HMT forests, consisting mainly of roots and rhizomes of dwarf shrubs, is abundant. Yet its respiration

seems to be much less intensive than that of the above-ground biomass.

If that the estimations presented above are somewhere near correct, the situation prevailing in HMT forests is unfavourable for net primary production. The ecological reasons for this include the long winter and the comparatively high temperatures under the snow, particularly in the humus, which result in relatively intensive respiration. The summer temperatures of the humus, being relatively low, are similarly unfavourable for biological activity, so that the biomass of higher plants present in the humus becomes relatively large compared with the above-ground, photosynthesizing biomass. All this also affects the net production of the trees, which is known to be small, particularly in the older HMT forests.

Ecological investigations of the HMT forest in Kuusamo are continuing. One of the present authors, E. Mäenpää, intends to concentrate on the photosynthesis and the CO_2 economy of this ecosystem, thereby hoping to obtain a more complete picture of the HMT ecology outlined above.

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